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Recovery of target bryophytes in floating rich fens after 25 yr of inundation by base-rich surface water with lower nutrient contents

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Abstract

Question: What are the changes in mineral-rich fens (H7410A) after 25 yr of improved surface water quality in a national park?

Location: Stobbenribben floating-fen complex in National Park Weerribben-Wieden, the Netherlands.

Methods: Bryophyte species composition, peak above-ground biomass and vascular plant nutrients, as well as electrical conductivity of various layers in the peat were measured between 1988 and 2013.

Results: The eutrophic moss *Calliergonella cuspidata* clearly decreased in aerial extent over the 25-yr study, especially near the ditch supplying base-rich surface water to the fen. In contrast, the characteristic rich fen species *Scorpidium scorpioides* expanded locally near the ditch. In the rich fen zone, peak above-ground biomass decreased from ca. 1000 to 250 $g{\cdot}m^{-2}$. Also, foliar N:P ratios in vascular plant tissues increased from 16 to more than 22 $g{\cdot}g^{-1}$, which clearly point to lower P availability over time. Improved surface water quality probably also promoted persistence of rich fen habitats in a different way. A large part of the rich fen peatland in 1988 changed into *Sphagnum* peatland by 2013, probably due to the reduction of base-rich water from below the floating root mat. This mat had become ca. 35 cm thicker in the past 50 yr. However, in areas closer to the ditch, rich fen species persisted, due to inundation with base-rich water during high water periods. Base-rich water probably no longer comes to the surface through the floating root mat, but more likely from the ditch.

Conclusions: Water quality improvement can be important in the long-term re-establishment of target fen species. Also, local inundation can be helpful if regional groundwater access becomes limited. In the national park, rich fens are more threatened than *Sphagnum* peatlands. This study suggests that the rich fen stage can be maintained, and succession towards *Sphagnum* peatland prevented, with occasional inundation with high pH, nutrient-poor water.

Introduction

Mineral-rich fens are threatened in Europe by acidification and eutrophication (Kooijman 1992; Gunnarson et al. 2000; Heino et al. 2005; Juutinen 2011; Lamers et al. 2015), and are protected by the EU Habitat directive (European Union 1992). Mineral-rich fens have become very rare, and well-developed fens with *Scorpidium* spp. may cover less than 10 ha in the Netherlands (Cusell et al. 2013a). Mineral-rich fens are characterized by high plant diversity, including EU habitat directive species such as *Liparis loeselii*, and many brown moss species (Sjörs 1950; Succow & Jeschke 1986; Hallingbäck & Hodgetts 2000; Vitt & Wieder 2009). Bryophytes are not only important in terms of biomass dominance, but also good indicators of environmental conditions, because they have no roots and are only one cell layer thick (Proctor 1982). In fact, the bryophyte layer is a sensitive indicator of environmental change in rich fen ecosystems (Sjörs 1950; Gorham et al. 1987).

Many rich fens are threatened by acidification (e.g. Clapham 1940; Koerselman et al. 1990; Van Wirdum

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1991; Van Diggelen et al. 1996; Soudzilovskaia et al. 2010; Lamers et al. 2015). To maintain sufficient acid neutralization capacity and ensure survival of rich fen species, input of calcium and bicarbonate-rich water is needed (Hajek & Adamec 2009; Soudzilovskaia et al. 2010). When access of base-rich water to the fen surface is reduced, rich fen mosses are replaced by *Sphagnum* species, and these mosses actively acidify these wetlands (Clymo 1963; Kooijman & Paulissen 2006). In many industrialized countries, high atmospheric deposition also contributes to acidification (De Haan et al. 2008). This process may result in approximately 1.5 times higher amounts of buffer components needed to sustain a suitable pH (Kooijman 2012). However, in many fens, supply of base-rich water has become limited. Groundwater input has been reduced in many areas, due to extraction for drinking water and agriculture (Schot & Molenaar 1992; Van Loon 2010).

Many rich fens are also threatened by eutrophication, which is a problem in densely populated countries with intensive agriculture (Lamers et al. 2015). Many rich fens are P-limited (Wassen et al. 2005). Eutrophication generally leads to an increase in biomass production and changes in plant species composition, especially in the bryophyte layer. In many rich fens, characteristic brown-moss species such as *Scorpidium scorpioides* and *S. cossoni* have been replaced by more eutrophic species, such as *Calliergonella cuspidata* (Kooijman 1992, 1993). In the 1980s, even the most biodiverse rich fens of the Netherlands contained moss species of more eutrophic habitats (Verhoeven et al. 1988; Van Wirdum 1991). Meanwhile, measures have been taken to improve water quality and decrease eutrophication in many wetland nature reserves, especially eutrophication with P (Lamers et al. 2015). In Weerribben-Wieden National Park, such measures included wastewater treatment and redirection of regional and local water flows, to reduce input of nutrients to natural systems. Although concentrations of total P did not change between 1982 and 2000, phosphate concentrations in the main channels decreased from 1–2 to 0.5–1.0 $\mu mol \cdot L^{-1}$ (Cusell et al. 2013a).

The goal of this study was to evaluate 25 yr of changes in bryophyte species composition, nutrient availability and base status in response to water quality improvement, in one of the largest and best-preserved rich fen complexes in the Netherlands. Rich fen studies over such periods are becoming more common (Van Diggelen et al. 1996, 2015; Gunnarson et al. 2000; Juutinen 2011), but are not always conducted by the same researcher, and only address environmental changes in e.g. base status and nutrient availability, to a limited extent. In our study, we compared detailed surveys of the bryophyte layer in 5 m × 5 m grid cells in one of the fens, undertaken by the first author in 1988 and 2013. To analyse changes in nutrient status, peak above-ground biomass and vascular plant nutrient concentrations were measured in the rich fen zone in 1984, 1990, 2005, 2010, 2011 and 2012. Changes in base status in various peat layers were studied in various years using measurements of electrical conductivity as a proxy.

Methods

Study area

The Stobbenribben fens are located in Weerribben-Wieden National Park (eastern Netherlands), in one of the largest wetland areas in NW Europe (Fig. 1). The climate is temperate-humid, with 800 mm rainfall, evenly distributed over the year. The national park is surrounded by low-lying agricultural polders; during wet periods, water is pumped from these polders into the park to ensure constant water levels in the agricultural areas. Inside the park, water levels are also maintained more or less constant through water control structures, but are allowed to fluctuate 10 cm between 0.83 and 0.73 m below mean sea level (Cusell et al. 2013a).

The Stobbenribben consists of a few adjacent rectangular ponds of ca. 20–40 m width and 200 m length, created by cutting the *Carex* peat around AD 1900 (Van Wirdum 1991). Depth of the ponds to the Pleistocene sandy underlayer is ca. 2.5–3.0 m. Kuiper & Kuiper (1958) mentioned the site as a good example of floating fens, with many characteristic rich fen species, such as *S. scorpioides* and the EU Habitat directive species *Liparis loeselii*. The fens are annually mown with small machines to prevent establishment of shrubs and trees (Cusell et al. 2013a).

Hydrology of the fen complex was studied in 1970–1980s by Van Wirdum (1991). To the southeast, this fen complex borders an agricultural polder, which was drained in the 1950s and is several meters lower than the fens themselves (Fig. 1). As a result of their relative elevation, the fens are subject to downward water movement (infiltration) of ca. 1–2 $m \cdot yr^{-1}$. The water loss is far larger than the precipitation surplus, and compensated by lateral inflow of surface water from a ditch at the NE side of the fens. This water flows beneath and through the floating root mat. Towards the SW end, the fens are hydrologically isolated with peat ridges, and base-rich ditch water becomes increasingly mixed with rain-water. As a result, the fens generally show a vegetation gradient from brown moss communities with *S. scorpioides* closer to the ditch to *Sphagnum*-dominated vegetation in the more isolated parts of the fen (Van Wirdum 1991).

In the 1980s, base-rich (ditch) water, needed to sustain the rich fen vegetation, was probably mainly supplied to

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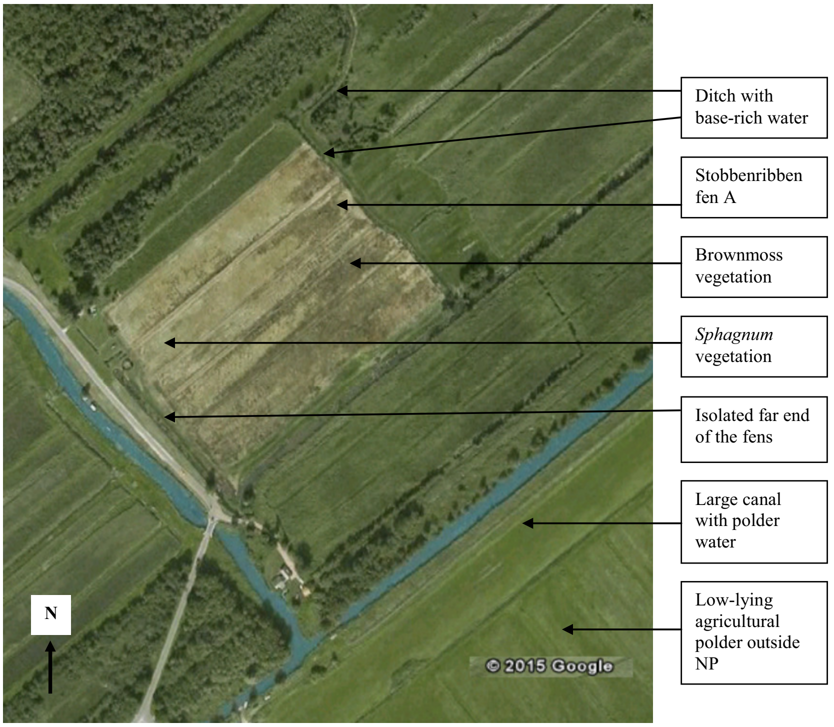

Fig. 1. Location of the Stobbenribben Fen complex in National Park (NP) Weerribben-Wieden. The dark brown colours in the fen complex indicate rich fen (brownmoss) vegetation dominated by Scorpidium scorpioides, the lighter areas are Sphagnum peatland dominated by S. palustre. The length of the fens is 200 m.

the fen surface from below the floating root mat, through gaps in the young layer of bryophyte vegetation (Van Wirdum 1991). However, occasional flooding with ditch water after heavy rain was reported, especially in areas close to the ditch (Bergmans 1975; Van Wirdum 1991; Kooijman 1993). The chemical composition of ditch water varies between seasons and years, depending on the amount of rain and input of water pumped in from the surrounding agricultural polders. Water moving out of the polders usually has relatively high calcium and bicarbonate content (Cusell et al. 2014a). However, polder water is also rich in nutrients, especially P.

Various measures have been applied to improve water quality since the 1970s. The major surface water inlet of the national park has been shifted from relatively eutrophic rivers to the much cleaner Lake Vollenhoven. Also, water purification facilities have been constructed, and P input from urban areas has decreased (Cusell et al. 2013a). Local measures to improve water quality and increase supply of base-rich ditch water were taken in 1992 (Schouwenberg & Van Wirdum 1997). The flow of water to the ditch in the Stobbenribben fen complex was redirected, leading to a longer pathway for nutrient removal. Also, within this project, the local ditch at the NE side of the fen complex was cleaned and enlarged.

Survey of the bryophyte layer

In one of the fens (Fen A), a detailed survey of the bryophyte layer was conducted in Oct 1988. The fen was divided in 200 grid cells of 5 m × 5 m, in 40 rows of five grid cells each. Unfortunately, in the last rows close to the ditch, six grid cells with unmown reed swamp, dominated by *C. cuspidata*, were inaccessible and thus not studied. In each grid cell, all bryophyte species present were noted; the total number of bryophyte species was 47. Bryophyte nomenclature is according to Van Tooren & Sparrius (2007). Cover values were adapted from Tansley (1946) and estimated on a scale from 1–5 (rare, frequent, common, co-dominant and dominant, respectively). The survey of the bryophyte layer was repeated in May 2013, within all 200 grid cells.

Peak above-ground biomass and foliar N:P ratios in vascular plants

Living vascular plant biomass growing above the fen surface was measured in the rich fen zone at 25–50 m from the ditch in Jul in 1984, 1990, 2005, 2010, 2011 and 2012. The number of replicates varied between sampling years from three in 1984, to three to five in later years. In 1984,

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the three replicates consisted of ten different subplots of 20 m × 20 cm (Verhoeven et al. 1988). In later years, above-ground living phanerogam biomass was collected in plots of 25 cm × 25 cm. Samples were collected, dried and weighed. After weighing, samples were ground and used for analysis of foliar N and P. In 1984–1990, N and P content were determined with a method using H_2SO_4 destruction with salicylic acid, and in 2005–2012 with a CNS analyser and microwave destruction with HNO_3 (Westerman 1990) followed by element concentration analysis with ICP-OES (Optima 3000 XL, PerkinElmer, Waltham, MA, US). Foliar N:P ratios were calculated as $g \cdot g^{-1}$. Foliar N:P ratios are a well-established proxy to estimate whether N or P could be a limiting factor (Koerselman & Meuleman 1996; Güsewell 2004; Cusell et al. 2014a). N:P ratios of 14–16 indicate more or less balanced conditions, while values above 20 clearly suggest P limitation (Koerselman & Meuleman 1996; Güsewell 2004). For 2010, however, P content was negligible so that these ratios were not analysed.

Surface EC values

Electrical conductivity (EC) values in the peat are related to calcium and bicarbonate concentrations in the water (Van Wirdum 1991; Cusell et al. 2014b), so that EC values may be used as a proxy for base status. EC values also help to determine the origin of base-rich water. EC at 25 °C and surface pH were measured during the bryophyte survey in Nov 1988, with a field meter at the fen surface near the centre of each 5 m × 5 m grid cell.

The EC measurements were repeated four times under various hydrological conditions, three of them characterized by high inundation of the rich fen zone (Jul 2012, May 2013 and Oct 2014), and one by low inundation throughout the fen (Nov 2012). Redox sensors in the rich fen zone showed low redox potentials during measurements with high water, and high values during low water (see Appendix A in Mettrop et al. 2014).

Electrical conductivity depth profiles

The EC depth profiles are very suitable to track the flow of water in and below the floating root mat (Van Wirdum 1991), and may help to determine the origin of the base-rich water. EC depth profiles were measured with a metal stick of 2 m with EC and temperature sensors in the top, which was pushed through the peat for measurements at different depths (Van Wirdum 1991). EC measurements were automatically corrected for temperature, standardized at 25 °C, and transformed to standard values in $\mu S \cdot cm^{-1}$. EC depth profiles were measured to 100 cm depth, which is in the zone of open water below the floating root mat. Surface EC values could often not be measured with the stick, and were measured with a field EC meter.

The EC depth profiles were measured along transects in the centre of the fen in Jun 1973 (Touber 1973) and in Jun 1990, Jul 2012, May 2013 and Oct 2014. EC depth profiles were also measured in Nov 2012, but in only in the half of the fen closest to the ditch; the plots in this case included all 5 m × 5 m grid cells as well as all wet hollows not in the centre of the grid cells.

In 1973, unfortunately, only five EC depth profiles were available, partly because parts of the floating fen were inaccessible (Touber 1973; Bergmans 1975). In 1990 and 2012–2014, each transect consisted of 16–28 measurement points, divided over the entire length of the fen. For comparison, the fen was divided in ten zones of 20-m length, and mean EC values for each zone were calculated.

In Jun 1973, the EC depth profiles started at 10-cm depth, and in Jun 1990 at 20-cm depth. Also, in Jun 1990, EC was measured every 20- rather than 10-cm intervals. In 2012–2014, however, EC depth profiles were measured from 0–100-cm depth, at intervals of 10 cm. In addition to the actual EC values, the data were used to calculate a rough proxy for the relative contribution of ditch water.

Statistical analyses

For most statistical analyses, the fen was divided into four zones of 50-m length, which more or less followed the zonation patterns of the fen in 1988. Differences in the number of grid cells containing particular bryophyte species between 1988 and 2013 were tested with Pearson's chi-squared tests, with 1988 values as the expected frequency (Mason et al. 1994). Differences were considered significant with P-values below 0.05.

Since the original biomass data of 1984 could not be retrieved, peak living above-ground phanerogam biomass and foliar N:P ratios were assessed using only the mean values and SD (Verhoeven et al. 1988). It was thus not possible to test differences between measurement periods directly with GLM. Instead, the changes over time were tested with linear regression analysis, with year and mean value per sampling period as input values.

Differences in surface EC values were tested with two-factor GLM, with fen zone and measurement series (time) as independent factors using SAS (Cody & Smith 1987). Differences between individual mean values were *post-hoc* tested with LSMeans tests. In zone 3, the zone at 100–150 m from the ditch, rich fen species still occurred in 1988, but became dominated by *Sphagnum* in 2013. In this zone, surface EC values were generally lower than in other zones, which masked potential differences between 1988 and 2012–2014 in the two-factor GLM. To further test such

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differences, a one-factor GLM was applied for this fen zone separately, with time as independent factor.

Differences in EC depth profiles were tested for the three periods with complete profiles and inundation in the rich fen zone: Jul 2012, May 2013 and Oct 2014. Three-factor GLM were used, with the 50-m fen zones, time and depth as independent factors. Each factor turned out to be highly significant, as well as some of their interactions. However, general patterns with depth and fen zone were the same in all periods, as shown by the insignificant interactions between time × depth and time × zone. For a more general analysis of EC differences with depth and between fen zones, data from different periods were combined. Potential differences were tested with two-factor GLM, with fen zone and depth as independent factors, and *post-hoc* LSMeans tests. For the sake of clarity, this analysis was also done for each fen zone separately.

In June 1973 and June 1990, EC depth profiles were unfortunately incomplete, which made a direct comparison with the values of 2012–2014 impossible. For a rough estimate, five 20-m fen zones were selected for which data were available for 1973, 1990, 2012, 2013 and 2014 at 0–20, 20–40, 120–140, 160–180 and 180–200 m from the ditch. The data of 2012–2014 were combined to one mean value per fen zone per depth, to give the present situation equal weight to 1973 and 1990. We used the 20- and 40-cm depth measurements, partly because EC values in 1990 were only measured every 20 cm, but also because changes in water transport from below the root mat to the fen surface could be better detected in the upper layers, especially because inflow patterns below the floating root mat seemed more or less the same. Differences in EC values were tested with three-factor GLM, with time, depth and fen zone as independent factors.

Results

Vegetation changes between 1988 and 2013

In 1988, the moss layer of the Stobbenribben Fen consisted of a mosaic of rich fen hollows interspersed with poor fen hummocks (Fig. 2). The fen had a zonation pattern characterized by dominant bryophyte vegetation near the ditch including eutrophic species such as *C. cuspidata*, *Brachythecium rutabulum* and *Calliergon cordifolium* (Table 1). By 2013, these eutrophic bryophytes had decreased, with *C. cuspidata* dominant only in a small zone directly adjacent to the ditch. *B. rutabulum* and *C. cordifolium* also decreased.

In 1988, a large part of the fen, up to 100-m distance from the ditch, was dominated by the mesotrophic rich fen species *Scorpidium scorpioides*. Other rich fen bryophytes were also present, such as *Campylium stellatum*, *Fissidens adianthoides* and *Calliergon giganteum*. In 2013, the rich fen species more or less completely disappeared from the central part of the fen. However, *S. scorpioides* increased closer to the ditch, and partly replaced the eutrophic *C. cuspidata*. The rich fen species *C. stellatum* also disappeared from the central fen, but increased near the ditch, albeit in lower numbers.

In 1988, the central part of the fen, the area of 50–150 m from the ditch, was dominated by the intermediate fen species *Sphagnum subnitens*, together with *S. contortum*. By 2013, both of these species were replaced by the poor fen species *S. palustre*, which by then dominated almost 70% of the area. Other poor-fen species also increased, such as *S. magellanicum*, *S. capillifolium* and *Polytrichum commune*.

Decrease in biomass production and P availability over the past 25 yr

The decrease in eutrophic bryophytes after 1988 was accompanied by a decrease in above-ground vascular plant biomass production (Table 2). In 1984, peak standing crop amounted to more than 1000 $g \cdot m^{-2}$ in the rich fen zone dominated by *S. scorpioides* and *C. cuspidata*. In 1990, values in this area had decreased to ca. 500 $g \cdot m^{-2}$, and further decreased to ca. 250 $g \cdot m^{-2}$ in the last few years. Value of foliar N:P ratios increased. In 1984, foliar N:P ratios were about 16, but gradually increased over time to above 22.

Electrical conductivity values at the fen surface

In July 2012 (high-water period), water levels in the national park ranged around the maximum for several weeks, due to a prolonged wet period, and the rich fen zone was completely inundated, with water levels of 3–12 cm above the surface. At the time of these measurements, an open connection existed between the surface water of the ditch and the fen, over a length of ca. 10 m. In Nov 2012 (low-water period), water levels had gradually dropped after Sept to the minimum. Water levels in the ditch and fen were also low and the surface water in the ditch and fen was not connected. In May 2013 (high-water period), measurements were conducted 2 wk after the first rise to maximum water levels since Sept 2012, which lasted for about 1 wk. Water levels in ditch and fen were still relatively high, and the open connection between ditch and fen was ca. 0.5-m wide. In Oct 2014 (high-water period), measurements were conducted 10 d after the first rise to maximum water levels after a dry period of 2 mo. During the measurements, the rich fen zone was still partially inundated and anoxic, but the open connection between ditch water and fen surface was not more than a few cm. Mean EC of the ditch was 517 $\mu S \cdot cm^{-1}$ in Jul 2012, 353 $\mu S \cdot cm^{-1}$ in Nov 2012, 627 $\mu S \cdot cm^{-1}$ in May 2014 and 572 $\mu S \cdot cm^{-1}$ in Oct 2014.

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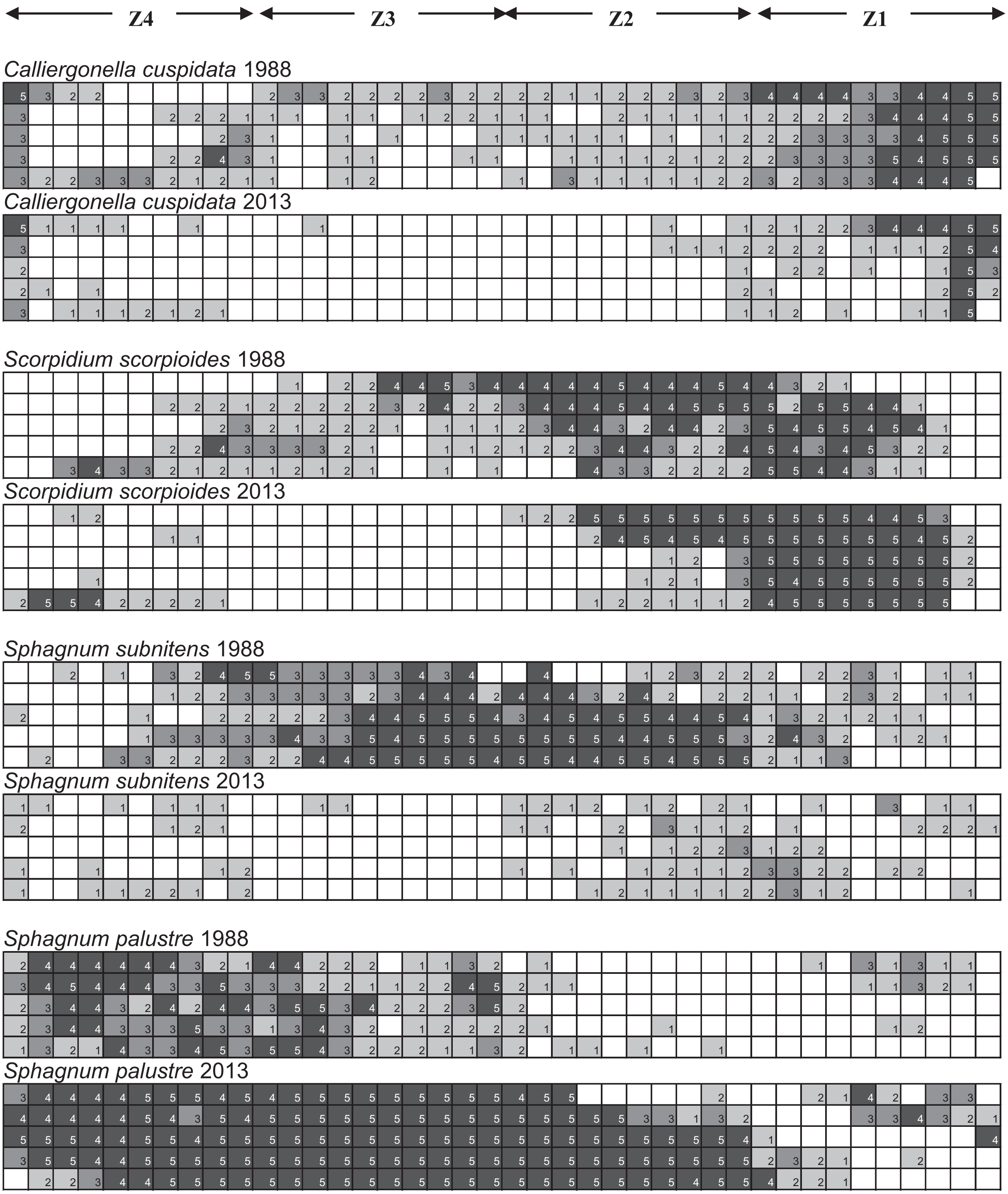

Fig. 2. Comparison of selected bryophyte species within the Stobbenribben Fen in 1988 and 2013 in 200 5 m × 5 m grid cells. The ditch, which supplies base-rich water to the grid cells, is represented toward the right of the figure. Z1 = zone 1, 0–50 m from the ditch at the right of the figure; Z2 = zone 2, 50–100 m from the ditch; Z3 = zone 3, 100–150 m from the ditch and Z4 = zone 4, 150–200 m from the ditch. 1 = rare (light grey); 2 = frequent (light grey); 3 = common (grey); 4 = co-dominant (dark grey) and 5 = dominant (dark grey).

In general, EC values at the fen surface decreased from the ditch to the more isolated end of the fen (Fig. 3, Table 3). High EC values above 400 μS·cm^{-1} were mostly present near the ditch in zone 1, where rich fen vegetation prevailed. However, temporal and spatial variation was rather large. In Nov 1988 and Jul 2012, EC values above

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Table 1. Presence (in percentage) of characteristic bryophyte species in the Stobbenribben in 1988 and 2013, in total or in particular fen zones of 50-m length, starting from the ditch at the NE side of the fen. Z1 = zone 1, 0–50 m from the ditch; Z2 = zone 2, 50–100 m from the ditch; Z3 = zone 3, 100–150 m from the ditch and Z4 = zone 4, 150–200 m from the ditch.

Bryophyte Species	1988					2013				
	Total	Z1	Z2	Z3	Z4	Total	Z1	Z2	Z3	Z4
Eutrophic Rich Fen Species										
Calliergonella cuspidata	78	25	21	15	12	32*	18*	5*	1*	10
Sphagnum squarrosum	68	11	21	24	12	1*	0*	1*	0*	0*
Brachythecium rutabulum	21	11	1	1	8	4*	4*	0	0	0*
Calliergon cordifolium	12	2	1	2	8	1*	1	0	0*	0*
Rhytidiadelphus squarrosus	9	3	0	0	6	3*	2	0	0	1*
Plagiomnium affine s.l.	8	4	1	0	4	6	2	0	0	1*
Drepanocladus aduncus	7	7	1	0	0	1*	1*	0	0	0
Mesotrophic Rich Fen Species										
Sphagnum subnitens	76	16	23	25	14	41*	12	17	1*	11
Campylium stellatum	72	16	24	21	11	46*	21	15*	0*	10
Scorpidium scorpioides	71	17	24	21	9	44*	22	16*	0*	7
Sphagnum contortum	64	7	21	22	15	23*	3*	6	2	12
Bryum pseudotriquetrum	50	14	14	15	8	42	24*	9*	0*	10
Fissidens adianthoides	39	18	16	4	3	14*	11*	3*	0*	1
Calliergon giganteum	23	10	3	7	4	15*	8	3	0*	4
Poor Fen Species										
Polytrichum commune	63	5	12	23	24	72	5	18*	25	25
Sphagnum palustre	62	7	7	24	25	83*	12	22*	25	25
Sphagnum fallax	58	7	4	24	43	69*	10	21*	22	16*
Aulacomnium palustre	40	4	3	18	15	22*	4	0*	5*	13
Sphagnum papillosum	17	0	0	6	11	19	0	0	5	14
Sphagnum capillifolium	5	0	0	2	4	20*	1	5*	12*	3
Sphagnum magellanicum	1	0	0	0	1	11*	0	0	2	10*

*Significant increase or decrease in number of grid cells between 1988 and 2013 in total or in a particular fen zone (chi-square tests; $P < 0.05$).

Table 2. Peak above-ground living vascular plant biomass and foliar N:P ratios in July in Stobbenribben in the rich fen zone with *S. scorpioides*, close to the ditch. Values are mean and SD in parentheses. The decrease in phanerogam biomass and increase in N:P ratio with time was significant for both factors ($R^2 = 0.79$ and 0.90, respectively).

Year	Vascular Plant Biomass ($g{\cdot}m^{-2}$)	Foliar N:P Ratio ($g{\cdot}g^{-1}$)
1984	1123 (241)	16.0 (1.8)
1990	512 (73)	19.1 (3.1)
2005	212 (136)	22.4 (2.2)
2010	187 (110)	
2011	229 (96)	23.7 (1.5)
2012	287 (74)	22.1 (1.1)

400 $\mu S{\cdot}cm^{-1}$ were relatively common in zone 1, but in Nov 2012, when water levels had been low for several months, lower values prevailed. In contrast, in May 2013 and Oct 2014, when the rich fen zone became inundated after a prolonged dry period, high EC values also occurred in zone 2. In May 2013, 82% of the grid cells with *S. scorpioides* had EC values above 400 $\mu S{\cdot}cm^{-1}$.

While temporal variation was rather large, there were no indications that the distribution of base-rich water near the ditch drastically changed between 1988 and 2012–2014. Near the ditch, the 1988 values actually fell within the range of values for 2012–2014, although we had only one set of measurements in 1988 and do not know whether EC values were high or low for that period. Also, in both periods, high EC values were only found near the ditch. However, in the central part of the fen, base status of the fen surface water probably fell. In 1988, many surface EC values ranged between 100–300 $\mu S{\cdot}cm^{-1}$, and values below 100 $\mu S{\cdot}cm^{-1}$ were measured in only 9% of the grid cells. These relatively high values point to at least some contact with base-rich water. In 2012–2014, however, EC values below 100 $\mu S{\cdot}cm^{-1}$ were very common. Also, in *S. palustre* vegetation, EC could often not be measured, due to lack of surface water. In the overall statistical analysis, differences in zone 3 between 1988 and 2012–2013 were not significant, due to much higher EC values in zone 1. However, when zone 3 was analysed separately, 1988 showed significantly higher values than all other years. These results suggest that contact of the peat surface with base-rich water is no longer common, and has actually diminished compared to the situation in 1988.

Table 3. Mean pH and EC values (μS·cm^{-1}) and SD at the fen surface in different measurement periods and different fen zones, starting from the ditch at the NE side. Zone 1–4 are each progressively 50 m more distant from the ditch, with zone 1 0–50 m from the ditch. Different letters indicate significant differences between fen zones and/or times ($P < 0.05$).

	Zone 1: 0–50 m from Ditch	Zone 2: 50–100 m from Ditch	Zone 3: 100–150 m from Ditch	Zone 4: 150–200 m from Ditch
pH				
Nov 1988	6.2 (0.3)^{c}	6.1 (0.4)^{c}	5.0 (1.0)^{b}	4.7 (0.7)^{a}
EC				
Nov 1988	342 (109)^{c}	177 (100)^{ab}	140 (50)^{a}	171 (41)^{a}
July 2012	396 (85)^{c}	184 (122)^{ab}	43 (-)^{a}	123 (48)^{a}
Nov 2012	264 (100)^{b}	95 (44)^{a}	-	118 (37)^{a}
May 2013	555 (59)^{d}	369 (224)^{c}	71 (33)^{a}	263 (176)^{b}
Oct 2014	530 (66)^{d}	226 (224)^{ab}	107 (19)^{a}	166 (75)^{a}

← Z4 → ← Z3 → ← Z2 → ← Z1 →

November 1988

Z4										Z3										Z2										Z1									
220	200	200	240	175									192	242	215	267	154	122	178	280	260	271	254	386	414	203	165	435	312	224	235	412	482	432	227	297	335	304	nd
255	140	160	175	160	145	128	226	165	149	329	155	145	131	164	118	134	131	148	126	137	116	171	158	197	100	162	113	163	132	141	102	170	130	228	345	422	425	415	nd
140	210	160	130	120	194	162	138	181	123	164	117	123	128	159	122	74	185	121	154	89	108	121	104	126	117	165	182	111	503	123	199	151	422	324	410	411	432	451	nd
120	230	210	155	135	183	125	155	130	146	171	170	92	98	150	84	82	147	123	86	102	98	82	126	155	123	200	175	101	367	413	367	386	427	390	418	416	364	396	nd
290	205	225	210	160	150	171	98	136	168	107	129	116	102	93	148	107	87	98	73	73	64	87	119	179	151	108	140	111	227	268	424	450	431	423	389	421	431	nd	nd

July 2012

114	73	65	63	51															43	41	48	228	272	309	282	306	295	303	302	297	337	359	356	374	387	395	429	392	390
78																							301	302	265	360	326	335	432	381	390	781	477	378	416	397	392	392	426
																										66	91	73	125	435	441	522	447	437	440	442	456	419	416
95																								50	66	69	71	61	152	350	216	350	520	437	380	452	417	411	397
188	182	175	163	171	161	157	154	116	83														61	61	88		78	60	204	297	275	227	258	348	306	353	384	430	nd

November 2012

	120	90																			52	76	119	119	135	92	134	232	170	270	293	304	238	278	389	299	362	320	346
																					54	68	79	119	138	140	189	217	160	227	182	256	278	43		54	61	373	371
																					52	71	65	85	51	102	61	69	127	260	189	279	458	233	153	314	285	337	95
92																					71	82	52	83	57	112	64	63	92	274	109	256	475	270	332	297	291	454	166
94	186	124																		60	57	50	50	107	81	86	68	77	92	141	284	290	170	292	221	324	288	117	345

May 2013

385	370	342	258	204			110	64			90			92	73	62	60	67	119	525	534	523	561	518	470	578	605	445	694	603	564	480	620	572	514	563	504	550	524
270						201	213	74		107	46	65	228	90	74	55	48	51	41	333	383	355	627	512	738	689	698	644	595	544	643	525	439	578	531	521	576	606	608
250						49	66	74	131	36	63	129	74	72	52	83	100	57	85	55	172	102	65	73	228	354	303	88	690	544	664	661	517	567	447	535	533	605	627
341	556		545			57	58	92	76	45	53	43	43	60	67	51	57	69	70	70	80	87	101	113	104	333	325	209	693	650	654	544	483	586	504	522	532	561	511
467	510	504	531	533	494	282	281	169	109	33	64	63	91	49	63	48	137	45	52	47	116	123	276	399	288	412	663	336	532	699	488	444	608	499	576	513	535	542	555

October 2014

321	304	290	272	215	187	122	100	192	152	88	107	132	102	134	92	102	101	90	134	216	285	305	388	378	450	474	487	493	535	558	540	540	574	566	569	585	594	580	490
345					138	194	198	111	105	120	103	106	109	143	115	105	99	105	107	118	153	135	99	300	200	440	221	419	528	514	477	530	514	451	570	555	574	602	586
298				99	100	99	93	120	87	110	63	91	96	92	108	115	155	102	110	108	82	102	106	81	115	239	120	124	329	488	508	511	537	567	563	561	565	605	430
188			114	135	92	112	86	104	103	115	121	84	163	129	104	93	129	81	96	113	108	96	244	109	150	166	140	200	285	408	468	527	510	540	551	588	563	575	555
208	280	261	162	154	151	121	123	121	141	81	88	126	110	91	109	99	81	108	105	116	109	109	147	148	185	168	167	191	336	269	321	469	475	525	525	554	595	605	562

Fig. 3. EC values (μS·cm^{-1}) at the fen surface in the 200 5 m × 5 m grid cells in the Stobbenribben Fen in Nov 1988, Jul 2012, Nov 2012 and May 2013. Z1 = zone 1, 0–50 m from the ditch; Z2 = zone 2, 50–100 m from the ditch; Z3 = zone 3, 100–150 m from the ditch and Z4 = zone 4, 150–200 m from the ditch. If no values are given, EC could not be measured due to lack of surface water. Grid cells are classified as very low (white; EC < 100 μS·cm^{-1}), low (light grey; 100–300 μS·cm^{-1}), intermediate (grey; 300–400 μS·cm^{-1}) and high (dark grey; >400 μS·cm^{-1}). July 2012 was a period with high rainfall and high water table, Nov 2012 a period with low rainfall and low water table, and in May 2013 water table had increased after heavy rain to maximum levels for the first time since autumn 2012. EC values in the ditch were 517 μS·cm^{-1} for July 2012, 353 μS·cm^{-1} for Nov 2012, 627 μS·cm^{-1} for May 2013, and 572 μS·cm^{-1} for Oct 2014.

Electrical conductivity depth profiles

In 1973 and 1990, the EC depth profiles did not include the depths 60–120 cm (Fig. 4). Also, it is not clear whether the values were relatively low or high during these time periods. Nevertheless, they can be used to trace inflow patterns of base-rich water from the ditch. The basic inflow patterns below the floating fen have probably not changed

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since 1991 (Van Wirdum 1991). Inflow below the root mat may seem higher in 1973 than in 2012–2014, but that may be due to relatively high EC values in the ditch. In terms of ditch water contribution, values at 100-cm depth were ca. 51–56% in the zone furthest from the ditch in Jun 1973 and 45–52% in Oct 2014.

June 1973

Depth	180–200	160–180	140–160	120–140	100–120	80–100	60–80	40–60	20–40	0–20 m
0	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd
10	168	210		234					576	480
20	152	159		288					459	636
30	243	189		459					597	606
40	312	264		405					513	588
50	261	339		324					675	678
60	384	351		498					696	675
70	399	407		543					663	582
80	416	417		501					603	597
90	432	456		492					513	606
100	408	450		543					465	537

June 1990

Depth	180–200	160–180	140–160	120–140	100–120	80–100	60–80	40–60	20–40	0–20 m
0	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd
20	161	101	146	142	82	228	219	223	468	371
40	161	132	171	165	122	246	251	291	473	406
60	219	263	254	258	203	333	395	437	467	462
80	223	292	284	351	288	371	374	435	447	459
100	228	309	315	358	374	374	346	418	454	420

July 2012

Depth	180–200	160–180	140–160	120–140	100–120	80–100	60–80	40–60	20–40	0–20 m
0				66			66	208	374	426
10	32	50	47	66	57	48	66	213	393	444
20	82	54	67	97	58	48	97	225	339	366
30	58	70	77	116	59	53	116	214	359	346
40	62	92	87	131	69	52	131	232	376	404
50	55	169	108	212	79	70	212	232	400	396
60	118	194	134	250	139	101	250	294	418	438
70	127	233	183	252	191	171	252	289	395	473
80	155	244	187	367	281	266	367	376	442	491
90	166	289	258	452	325	398	452	393	507	517
100	189	377	321	448	320	436	448	432	501	488

May 2013

Depth	180–200	160–180	140–160	120–140	100–120	80–100	60–80	40–60	20–40	0–20 m
0	94	49	77	80	54	85	80	573	530	529
10	73	40	77	65	50	45	65	477	325	298
20	88	42	87	77	55	36	77	439	337	274
30	53	47	116	125	54	34	125	384	337	341
40	57	48	130	154	101	53	154	340	295	364
50	79	94	131	237	139	110	237	294	299	326
60	108	103	146	233	245	136	233	326	322	353
70	129	130	202	294	283	216	294	358	327	359
80	138	146	185	265	260	258	265	366	321	407
90	167	198	227	305	242	274	305	339	362	445
100	132	205	237	305	246	251	305	351	350	421

October 2014

Depth	180–200	160–180	140–160	120–140	100–120	80–100	60–80	40–60	20–40	0–20 m
0		98	115	105	92	109	105	368	511	553
10	95	69	74	82	64	64	82	307	358	350
20	77	57	74	66	49	48	66	302	339	341
30	76	57	103	78	74	57	78	303	337	390
40	76	66	151	101	85	75	101	353	340	357
50	123	117	184	168	180	102	168	406	376	395
60	149	197	217	326	336	138	326	377	351	405
70	165	283	292	382	356	269	382	428	417	427
80	227	337	314	439	407	384	439	438	447	469
90	223	328	327	489	388	433	489	449	416	464
100	257	300	331	468	395	415	468	463	455	448

Fig. 4. EC values (μS·cm^{-1}) at the surface and at different depths (cm) in the floating root mat, in different parts of a transect through the centre of the Stobbenribben Fen. Distances are given in meters from the ditch, which is positioned to the right of the plots in the figure. Grid cells are classified as very low (white; EC < 100 μS·cm^{-1}), low (light grey; 100–300 μS·cm^{-1}), intermediate (grey; 300–400 μS·cm^{-1}) and high (dark grey; >400 μS·cm^{-1}). In June 1973, EC depth profiles were only measured in five parts of the fen, partly because the central part was inaccessible, and not at the surface. In July 1990, EC values were only measured at every 20-cm depth and not at the surface. In July 2012, May 2014 and Oct 2014, the rich fen zone was inundated. (Mean) EC values in the ditch were 800 μS·cm^{-1} for 1973, 516 μS·cm^{-1} for 1990, 517 μS·cm^{-1} for 2012, 627 μS·cm^{-1} for 2013, and 572 μS·cm^{-1} for 2014.

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In the upper layers of the floating root mat, the water was probably more base-rich in 1973 than in 2012–2014 (Fig. 5). At 20–40-cm depth, EC values were significantly higher in zones closer rather than farther from the ditch, but also significantly higher in the overall fen in 1973 and 1990 than in 2012–2014. Differences were also significant when expressed as percentage ditch water. In 2012–2014, EC values at 20–40-cm depth were always lower than in 1973 and 1990.

The EC values were examined to determine the source of the water at the fen surface. In zone 1, closest to the ditch, EC values were significantly higher at the fen surface than at 10-, 20- or 30-cm depth during the three flooded surveys (Jul 2012, May 2013 and Oct 2014) during inundation of the rich fen zone (Table 4). At the surface, the average contribution of ditch water amounted to 83%, but this sharply decreased to 63–60% at 10–30-cm depth. Below the floating root mat, around 90–100-cm depth, values increased again to 77% ditch water due to open contact with the ditch. In both May 2013 and Oct 2014, however, EC values at the fen surface were even higher than below the floating root mat.

Discussion

Water quality improvement and long-term conservation of protected area vegetation

In protected wetland areas, water quality improvement is a key aspect of maintenance and restoration of aquatic and semi-terrestrial ecosystems (Naiman et al. 1999; Nienhuis & Gulati 2002; Lamers et al. 2015). Ecosystems such as the Everglades in the USA and the Rhine River in NW Europe have been severely polluted from urban and agricultural sources, so that attention must be paid to water quality improvement as part of the restoration process (Rudnick et al. 1999; Nienhuis et al. 2002). In many countries, legislation such as the Clean Water Act in the USA and the Water Framework Directive in the EU has been

	Depth	m from ditch 180–200	160–180	120–140	20–40	0–20
June 1973	20 cm	152	159	288	459	636
	40 cm	312	264	405	513	588
June 1990	20 cm	161	101	142	468	371
	40 cm	161	132	165	473	406
2012–2014	20 cm	82	51	54	338	327
	40 cm	65	69	85	337	375

Fig. 5. Comparison of EC values at 20- and 40-cm depth in five different 20-m fen zones in 1973, 1990 and average in 2012–2014. Distances are given in meters from the ditch at the right in the figure. Grid cells are classified as very low (white; EC < 100 μS·cm^{-1}), low (light grey; 100–300 μS·cm^{-1}), intermediate (grey; 300–400 μS·cm^{-1}) and high (dark grey; >400 μS·cm^{-1}). Differences were not significant between depths, but highly significant ($P < 0.0001$) between fen zones and years. EC values in the ditch were 800 μS·cm^{-1} for 1973, 516 μS·cm^{-1} for 1990 and average 572 μS·cm^{-1} for 2012–2014.

Table 4. EC values, given as percentage ditch water, and SD at different depths in different fen zones, starting from the ditch at the NE side of the fen. Measurements of July 2012, May 2013 and Oct 2014, when the rich fen zone was inundated, were combined. Different letters indicate significant differences within a particular fen zone between particular depths (i.e. within a column; $P < 0.05$).

	Zone 1: 0–50 m from Ditch	Zone 2: 50–100 m from Ditch	Zone 3: 100–150 m from Ditch	Zone 4: 150–200 m from Ditch
n	23	14	13	13
EC 0 cm	83 (12)^{c}	22 (17)^{ab}	16 (4)^{ab}	15 (5)^{ab}
EC 10 cm	63 (13)^{a}	16 (12)^{a}	10 (2)^{a}	11 (4)^{a}
EC 20 cm	60 (10)^{a}	16 (12)^{a}	9 (2)^{a}	13 (3)^{a}
EC 30 cm	60 (10)^{a}	21 (13)^{ab}	10 (4)^{a}	13 (5)^{ab}
EC 40 cm	62 (12)^{a}	27 (17)^{b}	12 (4)^{ab}	16 (9)^{ab}
EC 50 cm	65 (14)^{a}	36 (15)^{b}	20 (9)^{b}	21 (10)^{b}
EC 60 cm	67 (14)^{a}	48 (16)^{c}	31 (16)^{c}	28 (10)^{bc}
EC 70 cm	69 (14)^{ab}	56 (15)^{cd}	42 (14)^{d}	36 (15)^{c}
EC 80 cm	75 (15)^{b}	64 (15)^{cd}	53 (15)^{e}	41 (15)^{cd}
EC 90 cm	77 (16)^{b}	72 (16)^{d}	61 (15)^{ef}	44 (14)^{d}
EC 100 cm	77 (14)^{bc}	72 (15)^{d}	63 (16)^{f}	48 (19)^{d}

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implemented recently (Naiman et al. 1999; European Union 2000). In many areas, vegetative recovery is still lagging, but some ecosystems have shown signs of renewed vitality after reduction of water pollution (Makarewics & Bertram 1991; Nienhuis et al. 2002). In small lakes, improvement of water quality may lead to restoration of functional attributes such as healthy macrophyte vegetation, including re-establishment of *Chara* species (Bootsma et al. 1999). In our rich fen study, a vegetation shift over 25 yr towards the original vegetation type indicates that some functional attributes can also be regained by reducing water pollution. In particular, low availability of P is a desirable state for rich fens (Wassen et al. 2005). The decrease in plant productivity and increase in foliar N:P ratios of vascular species to values above 22 indeed shows that P has become a limiting factor over time in our study fen (Koerselman & Meuleman 1996; Güsewell 2004). The idea that Stobbenribben Fen is currently P-limited is further supported by the results of fertilization experiments in the fen complex, which show that vascular plant biomass increases with application of P, but not with N (Cusell et al. 2014a).

Long-term hydrological, water quality and vegetation changes with peat mat development

Despite the improvement in surface water quality in the national park and rich fen area, a portion of the rich fen turned into *Sphagnum*-dominated peatland. Rich fen vegetation is generally replaced by *Sphagnum* spp. when the peat mass is exposed to less base-rich water (Clapham 1940; Clymo 1963; Soudzilovskaia et al. 2010), although this process could be altered by high atmospheric deposition of acidic precipitation (Berendse et al. 2001; Limpens et al. 2003; Kooijman 2012). Over time, peat layers grow thicker, and the surface becomes more isolated, blocking access of base-rich water from below the mat. A palaeoecological reconstruction of the succession in zone 2 of our study fen suggests that the peat layer has become 35-cm thicker in ca. 50 yr (A.H. Fabers, B. van Geel and A.M. Kooijman, unpubl. data). Such a layer may effectively reduce the flow of base-rich water from below the floating root mat to the fen surface, as suggested from the decrease in EC values in the upper part of the fen over the past decades. Weak spots in the root mat could still provide access to base-rich water, but a detailed survey of EC depth profiles in all hollows in Nov 2012 suggests that the mat no longer allows base-rich water to rise to the surface.

Despite on-going succession, rich fen bryophytes are locally expanding in the Stobbenribben. In the SE fen of the Stobbenribben complex, rich fen bryophytes even increased from ca. 60% to 90% (1973 vs 2012: Van Wirdum 1991 and this study, respectively), while *Sphagnum* communities decreased from ca. 40% to less than 10% (1973 vs 2012: Van Wirdum 1991 and this study, respectively). Currently, the SE fen is largely occupied by dark brown *Scorpidium* vegetation (Fig. 1). While it is clear that rich fen vegetation persists in regularly inundated areas, a debate has started as to whether this situation is due to the general raising of the water table inside the fen, which has open connections with the ditch below the floating root mat, or superficial flooding with ditch water. Although occasional flooding of the Stobbenribben has been reported (Bergmans 1975; Van Wirdum 1991; Kooijman 1993), this flooding was expected to play a minor role in floating fens, which move up and down with the water table. In the past, the fen surface was probably primarily fed by base-rich water from below the floating root mat (Van Wirdum 1991). At present, however, this contact has probably become more restricted. Instead, superficial flooding may play a more important role. This idea is supported by EC values, which were higher at the fen surface than inside the floating root mat after flooding. In May 2013, EC values at the fen surface were even higher than below the floating root mat, which suggests that inflow of base-rich water from the ditch to the area below the root mat only began recently, so that high EC values did not extend further than 20 m from the ditch. At the fen surface, however, high EC values were found up to 60 m from the ditch, which supports the idea that the origin of the water is the ditch. Open connections with the adjacent ditch were indeed observed when the rich fen zone was clearly inundated. Due to downward water movement from the fen to the low-lying adjacent agricultural polders, water tables inside the fens are generally lower than in the ditch (Van Wirdum 1991), which at least allows inflow of water from the ditch into the fen. Other aspects of water dynamics in the system are still uncertain, for instance, how much of the flood water comes from the ditch, the relationship of EC values to reduction processes (Cusell et al. 2013b), and the route of base-rich water over the surface of the mat during flooding. Nevertheless, it is likely that the current source of the water in the fen is the ditch, which has recently improved in water quality.

Concluding remarks

This study shows that floating rich fens can be restored, even in industrialized countries with a high amount of human pressure, such as the Netherlands. One of the key factors is the gradual improvement of water quality over the past 25 yr, which resulted in a four-fold decrease in above-ground biomass production, a clear increase in P limitation, and replacement of eutrophic bryophytes such as *C. cuspidata* by the mesotrophic species *S. scorpioides*. The other key factors in the re-emergence of rich fen species

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may be high water levels and temporary inundation of the fens with base-rich surface water from the ditch, especially after improvement in water quality. Our results clearly indicate that rich fen vegetation can persist, despite ongoing succession, when the fen surface is occasionally inundated with mineral-rich but nutrient-poor water.

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